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Priming effect as determined by adding ^{14}C-glucose to modified controlled composting test

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Abstract

The development of new biodegradable packaging materials, especially biodegradable plastics, has created a need for biodegradability testing. The European standard for controlled composting test was used in this study for assessing if the addition of a test material results in excess CO_2 production in compost. This effect, designated as the priming effect, would give an erroneous result for biodegradation, which is based on CO_2 formation from the test material. Glucose was selected as a test substrate because it is the degradation product of starch and cellulose, which are major compounds of many packaging materials. Both ^{14}C-glucose and non-labelled glucose was applied to nine compost samples of variable stability and age from two weeks to 1.5 years. CO_2 and $^{14}CO_2$ evolution were measured during the incubation. Biodegradation of glucose in unstable composts (age $\leq$6 months) was negative and $^{14}CO_2$ evolution was poor, although the respective composts without glucose produced relatively high amounts of CO_2. It was concluded that a negative priming effect was observed in unstable composts, in which glucose remained mostly non-degraded and apparently inhibited the mineralization of native organic matter in the compost. In stable composts (age $\geq$6 months), biodegradation of glucose was high and approximately equal to ^{14}C-glucose mineralization, i.e., the composts showed no priming effect. Young composts were unsuitable for controlled composting test due to lack of stability. It is important to ensure that the compost inoculum used for the test is sufficiently stable.

Introduction

The priming effect is a phenomenon where humified portion of soil or compost starts to degrade at an accelerated rate after substrate addition (Tate 1987; Shen & Bartha 1996; Kuzyakov et al. 2000). Humus is always mineralized to some extent by its native microbial population, but contradictory evidence exists as to whether the mineralization is stimulated by substrate addition to the soil (Jenkinson 1971; Tate 1987). Priming effect can be studied by adding labelled and non-labelled substrate to soil or compost and comparing the biodegradation of the substrate (i.e. net CO_2 evolution) to $^{14}CO_2$ evolution (Shen & Bartha 1996). If the substrate inhibits rather than stimulates humus degradation, priming effect is negative (Shen & Bartha 1996; Kuzyakov et al. 2000). In various soil studies reviewed by Jenkinson (1971), either insignificant and transient, or no priming effect at all was observed. Tate (1987) concluded that priming effect is probably limited to special environmental conditions or to certain types of laboratory studies. However, according to Sharabi & Bartha (1993) and Shen & Bartha (1996, 1997) significant priming effect could be observed after the addition of glucose to the soil, although no priming effect occurred with other substrates. In earlier studies by Bingeman et al. (1953), Dalenberg & Jager (1981), and Sørensen (1974), glucose addition caused only a small and transient priming effect in soil.

In order to determine the biodegradability of test samples, standardized test methods have been developed (Pagga 1999). CO_2 evolution is measured from bottles filled with compost and the sample mixture, and from bottles with compost only, and biodegradation is calculated according to Equation (1) (European Standard prEN 14046 2000). It is assumed that organic matter in compost produces an equal amount of CO_2 during the test irrespective of the sample addition. However, if the test sample generates priming effect in the compost, the actual mineralization of the sample differs from the value resulting from Equation (1).

$$\text{Biodegradation} = \frac{m_1 - m_0}{m_{\text{theor.}}} * 100\% \qquad (1)$$

where,

m_1 = mass of CO_2 produced by compost and sample

m_0 = mass of CO_2 produced by background compost

$m_{\text{theor.}}$ = mass of CO_2 evolved from sample, if 100% is mineralized

To our knowledge, priming effect has not been studied in a compost environment with both labelled and non-labelled substrate together. However, biodegradation of corn starch and cellulose in the controlled composting test has been reported to be as high as 97.5–108.6% and 96.8%, respectively (Degli-Innocenti et al. 1998). These results probably indicate a positive priming effect in compost, in addition to unknown biodegradation.

In this study, priming effect was investigated in a modified, controlled composting test (European Standard prEN 14046 2000), i.e., the test was scaled down to 1/20 of the volume of the standard test. Glucose was used as a test substrate both in ^{14}C-labelled and non-labelled form. The influence of compost stability on priming effect was studied with nine compost samples of varying ages and origins. After incubation, the fate of radiolabelled glucose was studied by a stepwise extraction procedure.

Materials and methods

Compost samples

Five compost samples were obtained from Ämmässuo (ÄS) municipal composting plant, Espoo, Finland; three from Biolan (B) composting plant, Kauttua, Finland, and one was from VTT Biotechnology (VTT). Municipal solid waste is composted with wood chips in Ämmässuo, chicken manure with peat in Biolan, and vegetable and fruitwaste with bark, peat, and wood shavings in VTT. The ages of the compost samples and some chemical and physical characteristics of the composts are given in Table 1.

Glucose

Uniformly labelled D-^{14}C-glucose was obtained from NEN Life Science Products, Inc., Boston, USA. D-^{14}C-glucose in ethanol-water solution (9:1) had a specific activity of 9.62 GBq/mol, corresponding to a concentration of 3.7 MBq/ml, and a purity of >97%. Stock solution was made by adding 100 μl of the original D-^{14}C-glucose solution to 50 ml of deionized water. Non-labelled D-glucose was of analytical grade and was obtained from Merck KgaA, Darmstadt, Germany.

Modified controlled composting test with ^{14}C-labelled glucose

Experiments with ^{14}C-labelled glucose were performed under modified controlled composting conditions at 50 °C as explained by Tuomela et al. (2001). 2.9 g of non-labelled glucose was applied to each flask. The ratio of compost to glucose by dry weight was 6:1, and the wet weight of compost samples varied between 29 and 75 g. Approximately 5 000 Bq ^{14}C-glucose was added from stock solution to each flask, which represents 0.11 μg glucose per flask. The flasks with three (background flasks) or four replicates were incubated for 32 or 45 days in a water bath at 50 °C. The final number of replicates varied because some flasks were contaminated by the trapping liquid. Evolved $^{14}CO_2$ was collected in a vial containing 10 ml of 4.4 M KOH. 2 ml of KOH solution was mixed with 18 ml of OptiPhase HiSafe 3 scintillation liquid (Fisher Chemicals, England). Radioactivity was counted with a liquid scintillation counter (model 1411, Wallac oy, Turku, Finland) from duplicate samples. A special procedure was created for liquid scintillation counting due to background radioactivity caused by

Table 1. Some chemical and physical characteristics of the composts

Character	Compost								
	2 weeks ÄS[6]	2 months B[7]	3 months ÄS	3 months B	6 months B	6 months ÄS	6 months VTT[8]	7 months ÄS	1.5 years ÄS
pH	6.0	7.9	7.9	8.5	7.8	8.7	6.8	8.3	7.4
Conductivity (mS cm^{-1})	2.4	0.74	1.2	0.59	0.39	2.2	0.77	2.7	1.7
Dry solids (% ww^1)	59	34	51	44	30	51	23	59	36
Organic solids (% dw^2)	75	63	79	46	60	60	89	56	59
C/N[3]	20 (24)	ND[9]	16 (19)	ND	ND	11 (13)	23 (26)	11 (14)	10 (12)
HA/FA[4]	2.2	1.43	19	1.75	1.02	42	0.42	5.74	11.72
DOC[5] (mg g^{-1} ww)	15	ND	8.3	ND	ND	6.7	1.9	17.6	7.8

[1]ww = wet weight.
[2]dw= dry weight.
[3]The figure in brackets indicates the C/N ratio in compost after glucose addition.
[4]HA/FA = humic acids/fulvic acids.
[5]DOC = dissolved organic carbon.
[6]ÄS = compost from Ämmässuo.
[7]B = compost from Biolan.
[8]VTT = compost from VTT.
[9]ND = not determined.

^{40}K isotopes. The total CO_2 concentration in the trapping liquid was determined from duplicate samples by titrating 1 ml of KOH solution with hydrochloride acid (HCl), and biodegradation was calculated according to Equation (1). Priming indices were calculated according to Equation (2) (Shen & Bartha 1996). After incubation the flasks were stored at −20 °C until extraction.

$$P.I. = \frac{\text{Biodegradation}}{\frac{A_1}{A_{\text{tot}}} * 100\%} \tag{2}$$

where,

$P.I.$ = priming index

Biodegradation according to Equation (1)

A_1 = radioactivity of $^{14}CO_2$

A_{tot} = total radioactivity of ^{14}C-glucose

Controlled composting test in 5 l bottles according to the standard

The above modified controlled composting test with radiolabelled glucose was performed in 250 ml flasks. In order to compare these results to composting in the standard volume, biodegradation of glucose was also determined in 5 l bottles, with three compost samples from Ämmässuo (2 weeks, 3 months, and 6 months old). In addition, the background CO_2 evolution during ten days was also determined from Biolan compost samples. The test was performed at 50 °C as explained by Tuomela et al. (2001). Biodegradation was calculated according to Equation (1).

Mass balance extractions

Compost samples (7.5 to 9.5 g with three replicates) from each flask were weighed and stepwise extracted with artifical fresh water, 1,4-dioxane, and 1 M NaOH as explained by Tuomela et al. (2001). Radioactivity of the extracts was measured with a liquid scintillation counter, and the residue was air dried and combusted according to Tuomela et al. (1999) to determine residual ^{14}C.

Table 2. CO_2 evolution from glucose and from compost organic matter in flasks containing unstable compost

Character	Compost				
	2 weeks ÄS[2]	2 months B[3]	3 months ÄS	3 months B	6 months B
CO_2 evolution from background flasks (mg g^{-1} compost dw[1])	292	362	290	108	136
CO_2 evolution from glucose flasks (mg g^{-1} compost dw)	34	54	84	99	70
$^{14}CO_2$ evolution (% of ^{14}C-glucose)	4.7	11.3	15.1	15.1	12.5
CO_2 evolution from glucose, assuming that the same percentage of ^{14}C-glucose and unlabelled glucose is mineralized (mg g^{-1} compost dw)	12	28	37	37	31
CO_2 evolution from compost organic matter (mg g^{-1} compost dw)	22	27	47	62	40
CO_2 evolution from compost organic matter compared to background CO_2 evolution (% of background CO_2)	8	7	16	58	29

[1]dw = dry weight.
[2]ÄS = compost from Ämmässuo
[3]B = compost from Biolan.

Data analysis

Significant differences between mass balance extractions were tested by analysis of variance using Tukey's pairwise comparisons of means (rejection level = 0.05). In order to equalize variances, data were transformed according to Equation (3) before analysis of variance.

$$X' = \arcsin \sqrt{X} \tag{3}$$

Results

Unstable composts, i.e. composted less than 6 months, mineralized ^{14}C-glucose poorly, only 5–15% (Figure 1a), and the total CO_2 evolution from these composts with glucose addition also remained low (33–99 mg g^{-1} compost dry weight, Table 2). The background of the respective composts produced more CO_2, namely 108–362 mg g^{-1} compost dry weight (Table 2). Thus, biodegradation and hence priming indices ($P.I.$) of these unstable composts were negative (from -22 to -0.3), and correlated negatively with background CO_2 production (Figure 1b and 1c, Table 2), which means that glucose apparently inhibited the mineralization of compost organic matter. Glucose mineralization represented 45% of the total CO_2 evolution, and 55% of CO_2 evolved from compost organic matter, if it is assumed that the same percentage of non-labelled and labelled glucose was mineralized. Therefore, the mineralization of compost organic matter with glucose addition was only 7–58% of the mineralization of the compost without any addition (background) (Table

Table 3. The mass balance of ^{14}C in composts. The letters after the figures indicate the significant differences inside the column. Means inside the column marked by the same letter are not significantly different according to Tukey's test ($p < 0,05$). Number of replicates was mostly three, but in some cases two or four

Compost	% of total ^{14}C added				
	CO_2	Water	Dioxane	Alkali	Residue
2 weeks ÄS[1]	6.2 a	70.8 a	7.4 a	3.4 a	7.3 a
2 months B[2]	11.3 a	56.2 a	4.1 ab	4.2 a	6.0 ab
3 months ÄS	13.4 a	51.0 a	7.4 a	3.0 a	8.4 a
3 months B	15.1 a	57.3 a	3.6 ab	4.5 a	6.9 ab
6 months B	12.5 a	71.5 a	6.5 a	4.4 a	6.8 ab
6 months ÄS	43.3 b	13.9 b	1.5 bc	0.1 bc	6.6 ab
6 months VTT[3]	72.4 c	0.1 b	0.1 c	0.4 b	2.8 b
7 months ÄS	74.0 c	0.5 b	0.4 c	0.0 c	4.9 ab
1.5 years ÄS	65.5 bc	1.0 b	0.3 c	0.0 c	4.7 ab

[1] ÄS = compost from Ämmässuo.
[2] B = compost from Biolan.
[3] VTT = compost from VTT.

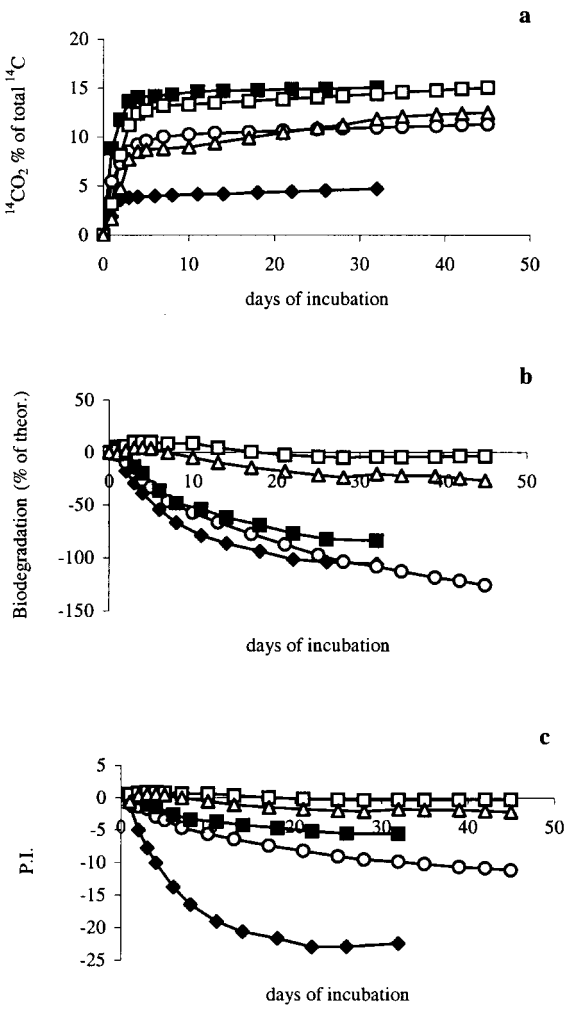

Figure 1. Unstable composts from Ämmässuo, age: 2 weeks (♦), 3 months (■), and from Biolan, age: 2 months (○), 3 months (□), 6 months (△). a. Mineralization of ^{14}C-glucose. b. Net CO_2 evolution (as percentage of the theoretical maximum of CO_2 production) of glucose. c. Priming index of glucose. Number of replicates was mostly three, but in some cases two or four.

2). Mass balance of radioactive carbon showed that the water fraction, representing non-degraded glucose, contained most of the radiolabel, namely 51–72% (Table 3). Consequently, as glucose addition inhibited the activity of unstable composts, glucose remained mostly non-degraded, and a negative priming effect was observed.

Stable composts, i.e. composted 6 months or more, mineralized 43–74% of ^{14}C-glucose (Figure 2a), and biodegradation of non-labelled glucose was 41–93%, respectively (Figure 2b). A substantial part of the glucose was mineralized during the first days of the experiment (Figure 2a and 2b). The average *P.I.* varied between 0.8 and 1.1 (Figure 2c), which means that glucose neither stimulated nor inhibited the degradation of compost organic matter. CO_2 evolution from the composts without any glucose addition (background) was significantly lower than that from unstable composts (Table 4). All the extracts and the residue together contained only 5–6% of ^{14}C-label after incubation, with exception of a compost from Ämmässuo composted for 6 months, which had also a great variation between the replicate samples: $^{14}CO_2$ evolution varied from 26 to 60% and ^{14}C-label in the water fraction from 37 to 1.5%, respectively (Table 3). The non-mineralized radioactive carbon was mostly bound to the residue, i.e. the humin fraction, and almost nothing to the alkali fraction, which represents humic and fulvic acids (Table 3).

Because the standard volume of the controlled composting test is from two to five liters, some parallel experiments were performed in 5 l bottles. We determined the biodegradation of glucose with three Ämmässuo composts, composted for 2 weeks, 3 months, and 6 months, and in addition the CO_2 evolution from the background of all three Biolan composts. The CO_2 evolution per mass unit was higher in 5 l bottles than in the smaller flasks with their respective composts (Table 4). The inhibition by glucose for all unstable composts in the smaller flasks was so severe that the compost microbial population could not recover (Figure 1b). In 5 l bottles (Figure 3), recovery of the

Table 4. CO_2 produced in ten or eleven days by composts. The comparison of 5 liters and 250 ml volume

Compost	250 ml flasks		5 l bottles	
	time (d)	CO_2 (mg g^{-1} VS[4])	time (d)	CO_2 (mg g^{-1} VS)
2 weeks ÄS[1] compost alone	11	289	10	328
2 weeks ÄS compost + glucose	11	33	10	63
2 months B[2] compost alone	10	283	10	527
3 months ÄS compost alone	11	268	10	314
3 months ÄS compost + glucose	11	100	10	432
3 months B compost alone	10	104	10	359
6 months B compost alone	10	72	10	148
6 months ÄS compost alone	11	60	10	73
6 months ÄS compost + glucose	11	208	10	382
6 months VTT[3] compost alone	11	78	–	ND
7 months ÄS compost alone	11	45	–	ND
1.5 years ÄS compost alone	11	81	–	ND

[1]ÄS = compost from Ämmässuo.
[2]B = compost from Biolan.
[3]VTT = compost from VTT.
[4]VS = volatile solids.

compost microbial population was observed after 16 days in 2-week old compost, but biodegradation was still negative on day 26 at the end of the experiment. In the 3-month old compost, negative biodegradation occurred only during the fourth and fifth days of the experiment and the final biodegradation of glucose was 102%, although in the smaller flasks biodegradation remained negative during the whole experiment. In the 6-month old compost, glucose was degraded in a similar way in both volumes (Figures 2b and 3).

All the parameters determined from the composts in our experiment had variation more due to their origin than to the stability of the compost (Table 1), although the ratio of humic acids to fulvic acids (HA/FA) and C/N ratio are considered to be maturity parameters for compost. The ratio HA/FA should increase, and C/N should decrease during compost maturation (Senesi 1989), however, in our study the HA/FA and C/N ratios did not correlate with the age of the compost (Table 1). Nor did these parameters correlate with the background CO_2 production (Tables 1, 2, and 4), and thus the stability of the compost. In fact the compost with the highest C/N ratio also had the highest initial biodegradation of glucose (Table 1, Figure 2b), although the most stable compost should have had the lowest C/N ratio. $P.I.$ was the only parameter that seemed to correlate with the stability, regardless of the origin of the compost (Figures 1c, and 2c, Table 2).

Discussion

In stable composts the mineralization was equivalent to the 47–83% ^{14}C-glucose mineralization in soil previously reported by Martin & Haider (1979) and Martin et al. (1974, 1978). ^{14}C-glucose mineralization of unstable composts was, however, close to the mineralization range of 18–28% in soil reported by Sharabi & Bartha (1993) and Shen & Bartha (1997), although they observed positive priming effect contrary to the negative priming effect seen in our experiments. A few authors have reported a small negative priming effect (Bingeman et al. 1953; Ezelin et al. 1996; Shen & Bartha 1997), but inhibition as high as we have observed, has not previously been described. The inhibition caused by glucose (Bingeman et al. 1953; Ezelin et al. 1996) or by starch or cellulose (Shen & Bartha 1997) was limited to one or two days at the beginning of the experiment. In the study of Wu et al. (1993), the biomass of the total microbial population increased after glucose addition. However, after large glucose additions of 1.25 g per 100 g soil, the amount of "native" soil organic matter degrading population simultaneously decreased. Glucose was almost totally mineralized during the first five days, but humus degradation probably slowed down, since half of the native population was erased in 20 days. Later, an excess of carbon dioxide was produced due to the accelerated death of the native biomass, and positive priming effect was observed (Wu et al. 1993). Death of

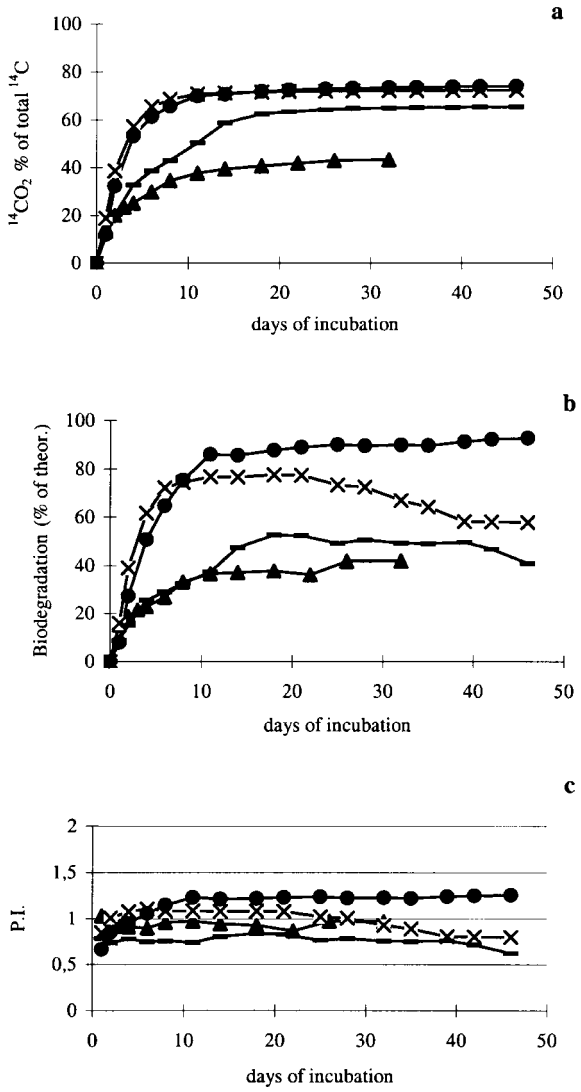

Figure 2. Stable composts from Ämmässuo, age: 6 months (▲), 7 months (●), 1.5 years (–), and from VTT, age: 6 months (×). a. Mineralization of ^{14}C-glucose. b. Net CO_2 evolution (as percentage of the theoretical maximum of CO_2 production) of glucose. c. Priming index of glucose. Number of replicates was mostly three, but in some cases two or four.

the native population after glucose addition may also have occurred in the study of Ezelin et al. (1996), because the total of cultured microflora of compost with glucose was considerably lower than that of control compost after two weeks of incubation.

When priming effect with glucose has been studied, the amount applied has varied from 0.025 g to 2 g per 100 g of soil (Bingeman et al. 1953; Dalenberg & Jager 1981; Sharabi & Bartha 1993, Shen & Bartha 1996, 1997; Sørensen 1974; Wu et al. 1993). Ezelin et al. (1996) applied 0.5 g glucose per 100 g of compost and Martin & Haider (1979) 5 g per 100 g soil as a maximal concentration. These concentrations are considerably lower than the concentration in our experiment (16.7 g glucose per 100 g compost). From these earlier studies Bingeman et al. (1953), Ezelin et al. (1996), Martin & Haider (1979), and Wu et al. (1993) reported an inhibitory or fatal effect caused by glucose. In the studies of Bingeman et al. (1953) and Ezelin et al. (1996) negative priming effect was small and transient, and in the study of Martin & Haider (1979) transient inhibition of glucose mineralization was observed only in alkaline soil. Thus, Wu et al. (1993) alone have discussed the phenomenon more closely, although compost organic matter decomposition was notably repressed due to glucose addition in the study of Ezelin et al. (1996). If a concentration of 1.25 g per 100 g soil or 0.5 g per 100 g of compost was enough to kill a substantial part of the native population (Ezelin et al. 1996; Wu et al. 1993), the concentration in our study could probably erase an even larger part of the compost biomass, the remaining population being so small that it could use only a small amount of the added glucose. Compost organic matter mineralization in glucose-containing flasks compared to that in background flasks shows that up to 93% of the original microbial population may have been killed after the glucose addition. If the remaining population recovers, there should be a positive priming effect from dead biomass as observed by Wu et al. (1993). Indeed, the final biodegradation of glucose with the 3-month old compost in 5 l bottles exceeded 100%. In comparison, the 6-month old compost started to degrade glucose immediately after addition, and the final biodegradation was 84%.

There are some other possible explanations for the negative priming effect. Glucose in such high concentrations may change C/N ratio unfavorably and repress the CO_2 evolution. There is evidence that nitrogen addition to immature compost or soil enhances O_2 consumption and CO_2 evolution, which means that decomposition of carbon compounds is increased (Inbar et al. 1988; Chantigny et al. 1999). Osmotic stress for microorganisms due to a high glucose concentration could end up being "toxic" effect (Kuzyakov et al. 2000); glucose can repress cellulose degradation (Stewart & Leatherwood 1976; Ezelin et al. 1996; Maheshwari et al. 2000) or protease production (Maheshwari et al. 2000), and glucose uptake of the thermophilic fungi can be saturated at 50 °C (Maheshwari et al. 2000). Nevertheless, all of these

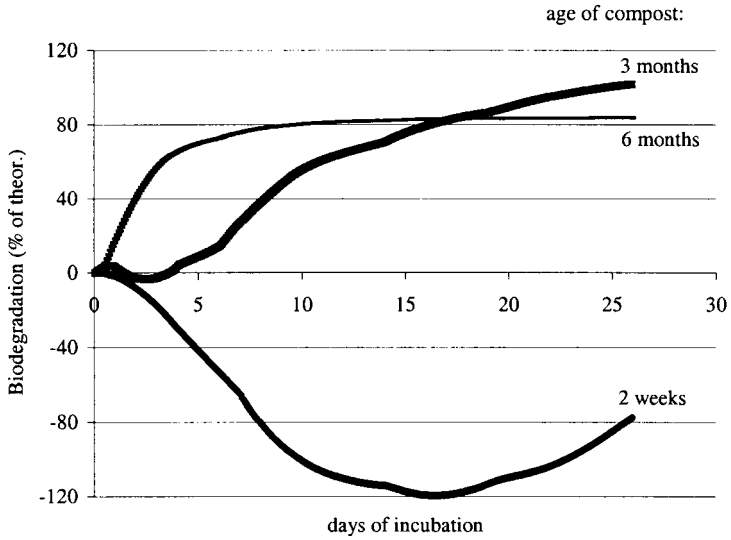

Figure 3. Net CO_2 evolution (as percentage of the theoretical maximum of CO_2 production) of glucose. Data from 5 l bottles. Composts from Ämmässuo, age: 2 weeks (♦), 3 months (■), 6 months (▲).

factors fail to explain why the glucose inhibition was observed only with unstable compost, and particularly, why the C/N ratio of the composts had no correlation to *P.I.* Furthermore, the rich population of the compost probably needs a much higher concentration of glucose than 0.76 M in order to kill the biomass by osmotic shock, although the dryness of the compost could amplify the negative effect (Itävaara et al. 2002; Wu et al. 1993). Nor did the study of Wu et al. (1993) confirm osmotic stress as the fatal agent for the native population of the soil. In order to explain the negative priming effect observed in our experiment, the principal aim is to reveal the essential difference between stable and unstable composts. *P.I.* correlates with background CO_2 production and the age of the compost, but does not correlate with parameters representing the amount of dissolved nutrients, such as conductivity and dissolved organic carbon (DOC). Thus, the differences in compost microbial population between stable and unstable composts may explain the differences in glucose degradation patterns.

None of the maturity parameters alone is appropriate to characterize the compost maturity (Forster et al. 1993; Inbar et al. 1993), and recent studies indicate that the ratio of HA/FA is inappropriate to characterize compost maturity because of high variation inside the group of substances called humic acids (Gonzăles-Vila et al. 1999; Veeken et al. 2000). However, the present results show that the priming index could be used as a parameter for maturity. When *P.I.* is approximately one, compost is stable, and when *P.I.* is significantly lower or higher than one, the compost population is not yet stable, and the compost is immature. European Standard (prEN 14046 2000) recommends that the compost inoculum used in the controlled composting test should be between 2- and 4-months old, and the compost should produce 50–150 mg CO_2 per g of volatile solids (VS) in ten days at 58 °C. According to our results, the age of the compost should be at least 6 months, if the inoculum from a full-scale plant is used, because compost maturation at full-scale is slower than at pilot- scale (Herrmann & Shann 1997). There was a high variation of *P.I.* between 6-month old samples of different origins, but it has been observed in other studies that the types of composting plant and waste and the efficacy of aeration are also important factors, along with the age for compost maturity and the formation of a stable population (Insam et al. 1996; Herrmann & Shann 1997; Carpenter-Boggs et al. 1998; Klamer & Bååth 1998; Tuomela et al. 2000). CO_2 production seemed to be a good parameter to describe the stability of the compost, and the cumulative value of ten days for the plain compost correlated well with *P.I.* The upper limit of the standard could possibly be lower, such as 100 mg CO_2 g^{-1} VS. Negative priming effect was observed with the 6-month old compost from Biolan, although its background CO_2 production remained below the upper limit.

In conclusion, the results obtained in this study suggest that the glucose addition erased a substantial part of the native population of unstable compost, as observed by Wu et al. (1993), or severely disturbed the enzyme system of compost microorganisms that degrade carbohydrates. The unstable microbial population of such a compost can be strongly affected by changing conditions, and it cannot be used as an inoculum for controlled composting test. The stable microbial community of matured compost readily utilized the added glucose without a priming effect, and the biodegradation was comparable to other studies. This observation may also have practical significance for the composting process. The compost microflora can be disturbed if large amounts of an easily hydrolyzable carbon source, such as starch, is added abruptly to immature compost. Future studies are needed to characterize the microbial community structure in different phases of composting, in order to explain more accurately the differences between stable and unstable compost priming effects, and to determine if this phenomenon concerns only glucose as a substrate.

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